



Effects of structural marsh management on fishery species and other nekton before and during a spring drawdown

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Abstract

We sampled experimental research areas in the Barataria Basin of Louisiana, USA to examine the effects of structural marsh management on habitat use by small nekton (< 100 mm Total Length or Carapace Width). The research areas consisted of two control (unmanaged) marshes and two impounded (managed) marshes; managed areas were surrounded by levees with water-control structures constructed by the U.S. Department of Interior, National Biological Survey. We sampled nekton with 1-m² enclosure samplers in 1995 just as a drawdown was initiated (March) and after two months of drawdown (May); a drawdown is an active management technique in which water is allowed to flow out of, but not back into, the impoundment. Samples were collected randomly from all available habitat types (shallow open water, submerged aquatic vegetation (SAV), and intertidal marsh) in the managed and unmanaged areas. In March, the densities of resident taxa (e.g., *Lucania parva* rainwater killifish and *Palaemonetes paludosus* riverine grass shrimp), which complete their life cycles within the estuary, were significantly greater in the managed areas compared to the unmanaged areas. The densities of most resident species were either similar in managed and control areas, or significantly greater in control areas during the drawdown (May). In contrast to residents species, the transient fishery species (e.g., *Callinectes sapidus* blue crab and *Farfantepenaeus aztecus* brown shrimp) reproduce outside of the marsh system and recruit to these areas as young. The densities of these transient species were significantly higher in unmanaged areas compared to managed areas during both sampling periods. We estimated standing crop (number or biomass of nekton per hectare of marsh area) by combining habitat densities with the area of different habitat types. The standing crops of transient species also were substantially greater in unmanaged than managed areas. We conclude that the restricted water exchange in marshes under structural marsh management diminishes recruitment and standing stocks of species that must migrate from coastal spawning sites to marsh nurseries. Even when water-control structures were open, the densities of these transient species were low inside managed areas. In contrast to the negative effect of management on transient species, the resident fish and crustacean populations seemed to flourish in the managed areas when a drawdown was not in effect. Following two months of a drawdown, however, the populations of residents appeared similar inside and outside managed areas. Increases in submerged aquatic vegetation (SAV) within ponds occurred outside the managed areas during the study period, but not inside managed areas. Because many resident species were closely associated with the SAV, the effect of management on SAV may have been responsible for the distribution patterns of resident species.

Introduction

The fishing industry in Louisiana is one of the largest in the USA, and commercial landings in this state

rank second only to those of Alaska (U.S. Department of Commerce, 1997). Unlike some regions of the country where fisheries are primarily supported by the continental shelf ecosystems, the coastal wet-

lands of Louisiana are directly used as nursery grounds by many fishery species. In particular, the young of penaeid shrimps and blue crabs (*Callinectes sapidus*) are closely associated with shallow, vegetated nursery habitats along estuarine shorelines (Minello, 1999; Zimmerman et al., 1999). Thus in the broadest sense, access to Louisiana's coastal habitats is critical for maintaining marine fishery productivity.

The loss of wetlands and fishery habitat along the northern Gulf of Mexico coast is a severe problem. The highest rate of coastal land loss occurs in Louisiana within the Mississippi River deltaic plain, where land was converted to open water at an average rate of $50 \text{ km}^2 \text{ yr}^{-1}$ between 1983 and 1990 (Britsch and Dunbar, 1993). This high land loss rate in Louisiana has been attributed to coastal submergence, canalization, salt water intrusion, leveeing the Mississippi River and channelizing and stabilizing its outlet, and wave erosion along exposed shorelines (Boesch et al., 1994; Penland et al., 1996; Turner, 1997).

Structural marsh management incorporates periodic drawdowns of the management area and has been advocated as one method to restore coastal wetlands, especially those marshes thought to be degraded by saltwater intrusion. Structural marsh management involves surrounding an area of marsh with levees and installing water-control structures to manipulate the hydrology of the enclosed marsh. A drawdown (or de-watering) of the managed area periodically is implemented to encourage the growth of emergent vegetation and the conversion of nonvegetated areas to marsh. This type of management has been carried out or proposed for thousands of hectares of coastal wetlands in Louisiana.

Marsh management plans often have been implemented without adequate monitoring to determine the consequences to fisheries and other resources. Where monitoring has been done, most studies have suffered from a lack of replication and suitable controls, the use of ineffective sampling gear, or the selection of non-random sampling sites that were restricted to a limited number of habitat types (Rogers et al., 1994). In addition, the effect of water-level fluctuations on nekton distributions among habitat types was usually not considered in the sampling design of these monitoring studies (Rozas and Minello, 1997). Nonetheless, most of the published literature on this topic suggests that structural marsh management and manipulation of marsh hydrology can restrict access to coastal wetlands and have a negative impact on fisheries production (e.g., Cowan et al., 1988; Herke

et al., 1992; Rogers et al., 1994), although not all studies reach this conclusion (Hoese and Konikoff, 1995). Scientifically defensible studies are needed to provide a basis for decision makers confronted with the contentious marsh management issue.

The overall objective of our research was to test the effects of structural marsh management on habitat use by juvenile fishery species and other small nekton before and during a spring drawdown of managed areas. We collected fishes and decapod crustaceans (mainly animals $< 100 \text{ mm}$ Total Length or Carapace Width) at experimental research areas constructed by the U.S. Department of Interior, National Biological Service (NBS); these areas were constructed specifically to examine the effects of structural marsh management on wetland loss and ecological processes. The specific objectives of our study were to: (1) compare density and biomass of fishery species between managed areas and unmanaged (control) areas, (2) examine the effects of a spring drawdown on the nursery function of managed marshes, and (3) identify and quantify nekton assemblages in all accessible habitat types (marsh, submerged aquatic vegetation or SAV, and nonvegetated bottom) in the study area.

Study area

Our study was conducted at the NBS marsh management study area located in the Barataria Basin of coastal Louisiana (Figure 1). Impoundments at the study area were constructed from fall 1991 through winter 1992 by NBS in cooperation with local landowners to assess the effects of structural marsh management in the Mississippi deltaic plain. Impoundments were constructed at two locations, Three Bayou Impoundment (TBI = 57 ha) and Little Lake Impoundment (LLI = 181 ha); and a reference or control location was established adjacent to each impoundment, Three Bayou Control (TBC = 30 ha) and Little Lake Control (LLC = 74 ha). These four experimental locations all contained both emergent marsh and open water (ponds). At the time we sampled, ponds occupied 56% (TBI) and 54% (LLI) of the area inside the managed areas and 39% of each control location.

The management regime used to control water levels in the managed areas (impoundments) is described in detail by Reed et al. (1997). Water level was manipulated in each managed area using one 1.05-m diameter, flap-gated culvert with installed stop-logs.

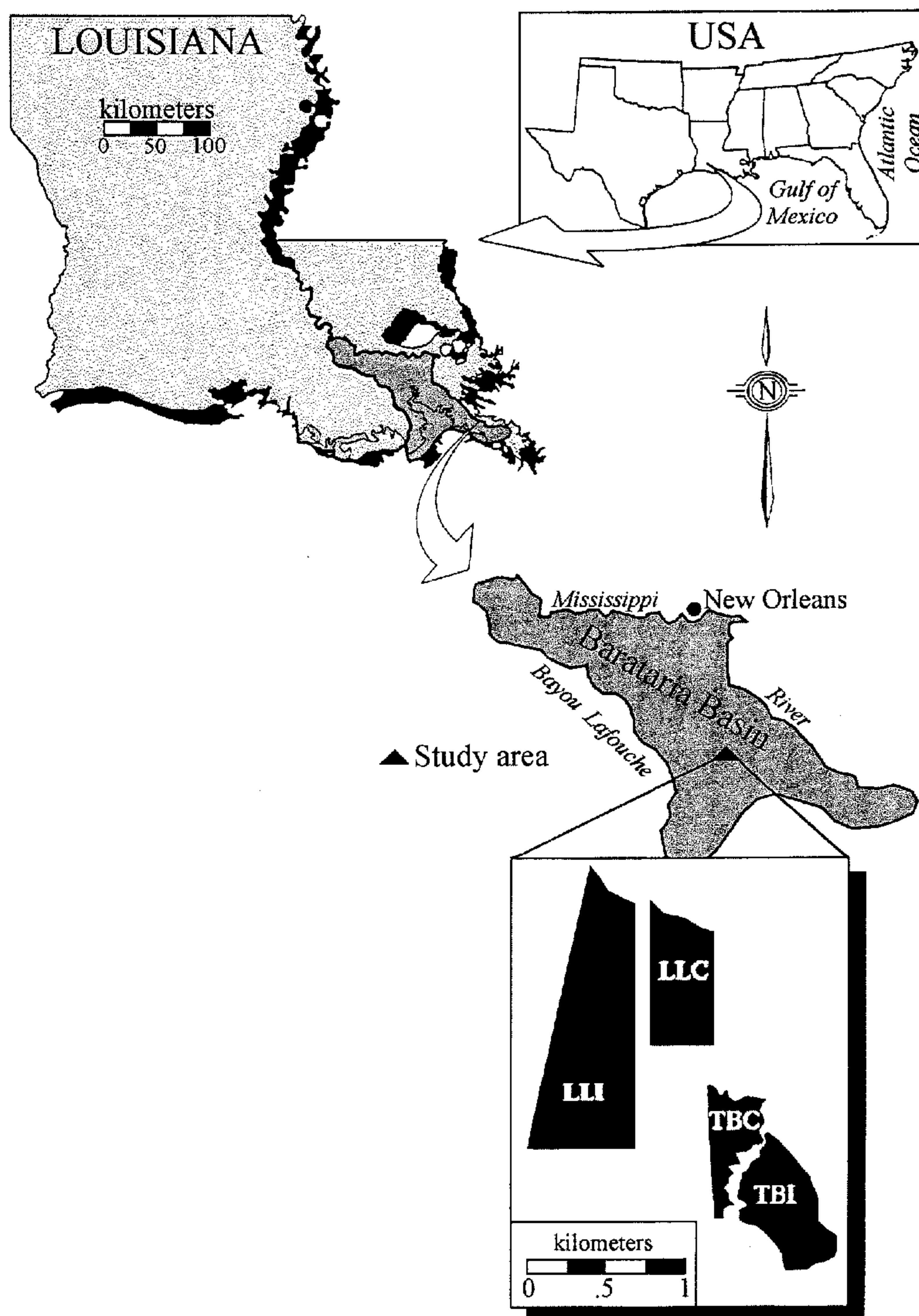


Figure 1. Map of the study area in the Barataria Basin. Samples were collected from four locations: Little Lake Impoundment (LLI), Little Lake Control (LLC), Triple Bayou Impoundment (TBI), and Triple Bayou Control (TBC).

We collected samples of nekton during two periods (March 21–24 and May 16–19) in the spring of 1995. These sampling periods targeted the time when a drawdown was initiated (March 16) and two months into the drawdown; these sampling times also coincided with an important period of recruitment for marine fishery species along the Louisiana coast when abundances of nekton in the study area were expected to be high. Just prior (5 days) to our March sampling effort, flap-gates on the water-control structures at each managed area had been open (since October 1994) and stop-logs set at 15 cm below marsh surface. Thus in March, our comparison of animal populations should represent differences between managed and unmanaged marshes under what is commonly considered relatively unrestricted tidal exchange (culverts open); although Rogers et al. (1992a) have shown that exchange is substantially restricted under these conditions. In fact, inflow ceases altogether when the water level outside the management area is below the crest of the stop-logs, as does outflow when water level inside the management area falls to the crest of the stop-logs. Flap-gates outside the structures were closed and stop-logs lowered to 30 cm below marsh surface on March 16 to initiate drawdown. During drawdown, water is allowed to flow out of the managed areas but not in; this procedure was in place until after we sampled in May. Therefore, comparisons in May should illustrate the effect of completely eliminating incoming water and organisms into managed marshes.

Methods

Three habitat types were present in managed areas and control areas. These habitat types included emergent marsh and two pond habitat types, nonvegetated mud bottom, and beds of submerged aquatic vegetation (SAV). We sampled all habitat types available to nekton using a variety of 1-m² enclosure samplers: a drop sampler (Zimmerman et al., 1984) and two types of throw traps (Kushlan, 1981). All of these enclosure devices have been shown to collect quantitative samples of small nekton in these habitat types (Rozas and Minello, 1997). The selection of gear type was mainly determined by water levels in the sampling areas.

Water levels in March were generally low. The emergent marsh was not flooded and was not sampled. The water depths were relatively shallow within the managed area, and an airboat was required to reach

sampling sites. In these areas, we used a 1-m² throw trap made with 0.61-m high walls of thin sheet aluminum. To minimize disturbance at sites prior to sampling, the airboat engine was turned off after motoring to a pond, and the craft was allowed to drift approximately 25 m before the throw trap was deployed. If water in a pond was too shallow for the boat to drift, then the sampler was thrown from a pond edge or from a small rubber raft used to get at least 25 m away from the airboat. Organisms were removed by sweeping the inside of the enclosure with a 1-mm mesh bar seine at least six times. Seining inside the sampler continued until three consecutive sweeps contained no animals, or until the sampler was swept at least 10 times. In control areas, where water depths were deeper, samples were collected using a 1-m² drop sampler following the method of Zimmerman et al. (1984). The device, a 1.14-m diameter cylinder (> 1 m in height) made of fiberglass and steel, was dropped from a boom mounted on a shallow-draft aluminum boat. The sampler was positioned over a sample site by two persons pushing from the boat's stern or by allowing the boat to drift over the sample area. The cylinder rapidly enclosed the sample area when released from the boom. We captured organisms trapped inside the cylinder using dip nets and by pumping water out of the enclosure and through a 1-mm mesh net. We removed any remaining animals by hand when the sampler was completely drained.

The water levels in May were high and the emergent marsh was flooded at both control locations and in the Little Lake impoundment. The drop sampler was used to sample this marsh because throw traps have low catch efficiencies at sites with rigid vegetative structure (Rozas and Minello, 1997). In ponds of both the controls and the managed areas, however, samples were collected using 1-m² throw traps with 1-m high walls constructed of 1.6-mm mesh nylon netting. These traps had a square frame made of steel bar (0.64-cm diameter) attached to the bottom of the net to make it sink rapidly through the water column and into the muddy substrate and prevent organisms from escaping beneath the net walls. A floating collar made of 1.91-cm diameter plastic pipe and attached to the top of the net kept the throw trap vertical in the water column after it was deployed. The sampler was thrown from the bow of a shallow-draft aluminum boat to sample sites in controls or deployed from an airboat or rubber raft in managed areas as described above. Animals were removed from these throw traps using clearing nets. The clearing nets were constructed of

1.6-mm mesh nylon netting attached to a 1.3×1.3 m frame made from 0.64-cm diameter steel bar. The throw trap was cleared by two persons by first placing the net against one side of the throw trap, and then carefully pushing the net frame under the throw trap and through the top layer of soft sediment. Once the clearing net was pushed beneath the throw trap, both the net and the trap were lifted out of the water. The throw trap was then removed from the clearing net, and the contents of the clearing net were carefully washed to remove any mud collected along with the sample.

Before removing animals from throw traps or drop samplers, we collected a water sample for turbidity and measured water temperature, salinity, dissolved oxygen, depth, and distance from edge of sampler to the marsh edge. The emergent marsh vegetation was mainly *Spartina patens*. In these samples, we clipped and removed marsh vegetation from the inside of the sampler to facilitate removal of animals. Beds of SAV in ponds were dominated by *Najas guadalupensis*, *Ceratophyllum demersum*, and *Myriophyllum spicatum*, although we also encountered *Bacopa monnieri*, *Eleocharis parvula*, *Paspalum vaginatum*, and the algae *Chara* spp. In pond samples, we felt around the bottom of the sampler to determine if SAV was present. If SAV was present, then we estimated its coverage within the sampler (0–100%), identified the species of plants present, and removed the vegetation from inside the sampler after vigorously shaking out any animals.

We selected sample sites using random numbers and a numbered grid placed over an aerial photograph of each location. Seven samples of emergent marsh (edge) were collected at each location if the marsh was flooded. Twenty-five samples were collected in ponds at each of the four locations in the following sequence. First, we sampled 20 randomly-selected sites at a location. If at least 7 samples of each pond habitat type (nonvegetated bottom or SAV) were collected in these first 20 samples, then we sampled five more randomly-selected sites for a total of 25 samples. However, if after we had taken 20 pond samples, less than seven samples of one of the pond habitat types were collected, then additional samples of the deficient habitat type were taken within randomly-selected grids to bring the total number to at least seven samples. This procedure insured that we collected at least seven samples of each available habitat type at each location (Table 1). The seven samples per habitat type were

collected within the first 20 samples at all locations except the LLC in March and May and TBC in May.

Nekton samples were preserved in the field in 10% formalin. Fishes and crustaceans were separated from detritus and plant parts in the laboratory, identified to species, and enumerated. The biomass for each species was determined by pooling individuals in a sample and measuring wet weight to the nearest 0.1 g. We calculated the standing crop (g ha^{-1}) for animals in each experimental location (TBI, TBC, LLI, LLC) by multiplying mean biomass or density values by the total area of habitat type present at each location and summing across habitat types. The NBS provided estimates of pond and marsh areas at each location from an analysis of aerial photographs. Our pond and marsh samples should provide good estimates of animal densities in these habitat types because sample sites were randomly selected within each experimental area, and throw traps and drop samplers provide quantitative samples of small nekton in shallow water (Rozas and Minello, 1997; Jordan et al., 1997). Using these data, we directly compared standing crop (in numbers and biomass) of fishery species between managed areas and controls.

Data analyses

March and May data were analyzed separately because some species of animals were only abundant enough to include in the statistical analyses for one month. We tested data collected from ponds for differences in mean animal density, biomass, and environmental parameters using a factorial Analysis of Variance (ANOVA, Table 2). Factors in the analysis were Location (TBI, TBC, LLI, LLC) and Habitat type (SAV and nonvegetated bottom), and there were at least seven replicate samples for each Location/Habitat combination. Contrasts were used within the main effect of Location and within the Location * Habitat interaction to test for impoundment effects. We did not include marsh-surface samples in this analysis because we did not sample the marsh surface in March and we sampled marsh in only one managed area in May. Because mean animal densities were positively related to the standard deviation, we performed a $\log(x + 1)$ transformation on these data prior to statistical analyses. Despite these transformations, the variances were unequal for taxa whose means equaled zero in at least one of the treatments. The data for these taxa were analyzed using the Games-Howell post-hoc test

Table 1. Number of samples taken in each habitat type at each area in March and May 1995. Samples were taken in marsh only when the marsh surface was flooded

Habitat type	Triple Bayou		Little Lake	
	Impoundment	Control	Impoundment	Control
<i>March</i>				
Total Marsh Samples	0	0	0	0
Total Pond Samples	25	25	25	25
Vegetated Pond (SAV Present)	8	17	12	15
Nonvegetated Pond (SAV Absent)	17	8	13	10
<i>May</i>				
Total Marsh Samples	0	7	7	7
Total Pond Samples	25	25	25	25
Vegetated Pond (SAV Present)	10	18	13	18
Nonvegetated Pond (SAV Absent)	15	7	12	7

Table 2. The Analysis of Variance (ANOVA) model used to compare throw trap data (animal densities) collected in March and May 1995. The factor Location had four levels (TBI, TBC, LLI, and LLC), and we used *a priori* contrasts within significant (0.05 level) Location effects to test for differences between impoundments and controls. The factor Habitat had two levels (SAV and Nonvegetated). A $\ln(x+1)$ transformation was used on the data prior to analysis. The dependent variables used in the examples presented here are total resident taxa and total transient taxa

Source of variance	March			May		
	df	SS	P	df	SS	P
Resident Taxa						
Location	3	53.753	0.0001	3	2.727	0.5336
Impoundment vs Control Contrast	1	39.558	0.0001			
Habitat	1	7.497	0.0077	1	16.213	0.0005
Location * Habitat	3	5.309	0.1621	3	1.078	0.8321
Error	92	92.993		92	113.741	
Transient Taxa						
Location	3	5.957	0.0001	3	13.599	0.0001
Impoundment vs Control Contrast	1	4.651	0.0001	1	11.215	0.0001
Habitat	1	1.254	0.0265	1	0.746	0.0898
Location * Habitat	3	1.942	0.0552	3	1.042	0.2572
Error	92	22.695		92	23.334	

for unplanned comparisons as recommended by Sokal and Rohlf (1981). Variables other than animal densities were not transformed. All tabular and graphical data presented in this paper are un-transformed means. We used SuperANOVA software (Abacus Concepts, Inc.; Berkley, CA) to do all analyses. An alpha level of 0.05 was considered statistically significant.

Results

We collected a total of 20 fish and 8 decapod crustacean taxa in March (Table 3). The marsh surface was not flooded in March, and therefore not sampled. Crustaceans were more abundant (62% of total) than fishes, although fishes accounted for slightly more of the total biomass (52% of total). *Palaemonetes paludosus*, *Callinectes sapidus*, and *Farfantepenaeus aztecus* (formerly *Penaeus aztecus*, Perez-Farfante and

Table 3. Mean densities, number m⁻², (± 1 standard error, S.E.) of animals collected in marsh ponds at impoundments and controls from four locations (TBI, TBC, LLI, and LLC) sampled in March and May 1995. Each mean and standard error are estimated from 25 samples, except in March LLC = 20 and in May TBC = 20 and LLC = 20 (Note: Means and standard errors were estimated using data from randomly-selected sample sites only.). The total number of animals collected is given for each taxon and major category (fishes and crustaceans). The relative abundance (RA) of taxa within each major category also is given when it is at least 1%. Results (P values) of ANOVA Contrasts comparing mean densities between managed and unmanaged areas are given for each taxa included in the analyses. NS=Location Main Effect in ANOVA was not significant ($p > 0.05$). Transient taxa identified with *

Taxa	TB		TB Control		LL		LL Control		Total	RA (%)	P
	Impoundment		Mean	S.E.	Impoundment		Mean	S.E.			
	Mean	S.E.							Mean	S.E.	
March											
Total fishes	4.1	(0.90)	3.3	(1.07)	5.9	(1.91)	1.1	(0.33)	358		0.0006
<i>Lucania parva</i> Rainwater killifish	2.3	(0.77)	0.6	(0.43)	0.6	(0.30)	0.5	(0.20)	101	28.2	0.0023
<i>Heterandria formosa</i> Least killifish	0.1	(0.08)	0.0	(0.00)	3.1	(1.60)	0.0	(0.00)	80	22.3	
<i>Cyprinodon variegatus</i> Sheepshead minnow	1.3	(0.51)	0.0	(0.00)	1.5	(0.55)	0.0	(0.00)	70	19.6	
<i>Poecilia latipinna</i> Sailfin molly	0.0	(0.04)	0.7	(0.42)	0.4	(0.25)	0.2	(0.14)	32	8.9	
<i>Gobiosoma bosc</i> Naked goby	0.2	(0.20)	0.8	(0.41)	0.0	(0.00)	0.1	(0.05)	26	7.3	
<i>Menidia beryllina</i> Inland silverside	0.1	(0.09)	0.1	(0.07)	0.0	(0.04)	0.1	(0.05)	8	2.2	
<i>Brevoortia patronus</i> Gulf menhaden *	0.0	(0.00)	0.1	(0.12)	0.0	(0.00)	0.2	(0.20)	7	2.0	
<i>Microgobius gulosus</i> Clown goby	0.0	(0.04)	0.2	(0.15)	0.0	(0.00)	0.0	(0.00)	7	2.0	
<i>Syngnathus scovelli</i> Gulf pipefish	0.0	(0.00)	0.2	(0.10)	0.0	(0.04)	0.0	(0.00)	6	1.7	
<i>Gobiosoma robustum</i> Code goby	0.0	(0.00)	0.2	(0.20)	0.0	(0.00)	0.0	(0.00)	5	1.4	
<i>Myrophis punctatus</i> Speckled worm eel *	0.0	(0.00)	0.2	(0.08)	0.0	(0.00)	0.0	(0.00)	4	1.1	
<i>Micropogonias undulatus</i> Atlantic croaker *	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.1	(0.10)	2		
<i>Gambusia affinis</i> Western mosquitofish	0.0	(0.00)	0.0	(0.00)	0.1	(0.06)	0.0	(0.00)	2		
<i>Gobionellus boleosoma</i> Darter goby	0.0	(0.04)	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	2		
<i>Paralichthys lethostigma</i> Southern flounder *	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	1		
<i>Achirus lineatus</i> Lined sole *	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	1		
<i>Syngnathus louisianae</i> Chain pipefish *	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	1		
<i>Fundulus chrysotus</i> Golden topminnow	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.04)	1		
<i>Fundulus similis</i> Longnose killifish	0.0	(0.00)	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	1		
<i>Citharichthys spilopterus</i> Bay whiff *	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	1		
Total crustaceans	2.2	(1.08)	2.6	(0.76)	17.7	(4.81)	1.1	(0.46)	583		0.0010
<i>Palaemonetes paludosus</i> Riverine grass shrimp	2.1	(1.08)	0.4	(0.24)	17.4	(4.78)	0.6	(0.40)	510	87.5	0.0001
<i>Callinectes sapidus</i> Blue crab *	0.1	(0.06)	1.4	(0.49)	0.0	(0.04)	0.5	(0.15)	48	8.2	0.0004
<i>Farfantepenaeus aztecus</i> Brown shrimp *	0.0	(0.00)	0.5	(0.28)	0.0	(0.00)	0.1	(0.05)	14	2.4	
<i>Palaemonetes intermedius</i> Brackish grass shrimp	0.0	(0.00)	0.0	(0.04)	0.1	(0.09)	0.0	(0.00)	4		
Family Cambridae Unidentified crayfish	0.0	(0.00)	0.0	(0.00)	0.1	(0.09)	0.0	(0.00)	3		
<i>Rhithropanopeus harrisii</i> Harris mud crab	0.0	(0.00)	0.1	(0.08)	0.0	(0.00)	0.0	(0.00)	2		

Table 3. (continued)

Taxa	TB Impoundment		TB Control		LL Impoundment		LL Control		Total	RA (%)	P
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.			
<i>Dsypanopeus texana</i> Gulf grassflat crab *	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	1		
<i>Macrobrachium</i> sp Unidentified rivershrimp	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	1		
<i>May</i>											
Total fishes	24.7	(6.22)	19.7	(4.12)	12.3	(2.50)	29.9	(7.15)	2124		NS
<i>Lucania parva</i> Rainwater killifish	13.0	(4.55)	10.8	(2.94)	3.4	(1.66)	20.7	(4.78)	1174	55.3	0.0004
<i>Cyprinodon variegatus</i> Sheepshead minnow	7.3	(1.08)	4.1	(2.70)	5.6	(1.19)	4.0	(2.12)	513	24.2	0.0001
<i>Menidia beryllina</i> Inland silverside	2.7	(1.48)	1.4	(0.33)	0.8	(0.61)	1.4	(0.83)	176	8.3	
<i>Heterandria formosa</i> Least killifish	0.0	(0.00)	0.0	(0.00)	2.0	(0.85)	0.0	(0.00)	50	2.4	
<i>Alosa alabamae</i> Alabama shad	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	2.3	(2.30)	46	2.2	
<i>Poecilia latipinna</i> Sailfin molly	1.1	(0.53)	0.1	(0.10)	0.0	(0.00)	0.9	(0.85)	46	2.2	
<i>Syngnathus scovelli</i> Gulf pipefish	0.1	(0.06)	1.3	(0.73)	0.0	(0.00)	0.1	(0.05)	30	1.4	
<i>Myrophis punctatus</i> Speckled worm eel *	0.0	(0.00)	0.6	(0.21)	0.0	(0.00)	0.2	(0.11)	21	1.0	
<i>Gobiosoma bosc</i> Naked goby	0.2	(0.16)	0.5	(0.31)	0.0	(0.08)	0.1	(0.05)	16		
<i>Microgobius gulosus</i> Clown goby	0.0	(0.04)	0.3	(0.20)	0.1	(0.06)	0.2	(0.20)	12		
<i>Gambusia affinis</i> Western mosquitofish	0.2	(0.10)	0.0	(0.00)	0.3	(0.12)	0.0	(0.00)	11		
<i>Fundulus grandis</i> Gulf killifish	0.1	(0.07)	0.1	(0.07)	0.0	(0.00)	0.0	(0.00)	6		
Family Gobiidae Unidentified goby	0.0	(0.00)	0.1	(0.07)	0.0	(0.04)	0.0	(0.00)	4		
<i>Microgobius thalassinus</i> Green goby	0.0	(0.00)	0.2	(0.11)	0.0	(0.00)	0.0	(0.00)	3		
<i>Anchoa mitchilli</i> Bay anchovy *	0.0	(0.00)	0.1	(0.05)	0.0	(0.00)	0.1	(0.05)	2		
<i>Micropterus salmoides</i> Largemouth bass	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.1	(0.07)	2		
Unidentified fish	0.0	(0.00)	0.1	(0.07)	0.0	(0.00)	0.0	(0.00)	2		
<i>Elops saurus</i> Ladyfish *	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.1	(0.05)	1		
<i>Fundulus jenkinsi</i> Saltmarsh topminnow	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
<i>Fundulus notli</i> Starhead minnow	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
<i>Lepomis cyanellus</i> Green sunfish	0.0	(0.00)	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	1		
<i>Lepomis marginatus</i> Dollar sunfish	0.0	(0.00)	0.1	(0.05)	0.0	(0.00)	0.0	(0.00)	1		
<i>Lepomis microlophus</i> Redear sunfish	0.0	(0.00)	0.1	(0.05)	0.0	(0.00)	0.0	(0.00)	1		
<i>Morone saxatilis</i> Striped bass *	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.1	(0.05)	1		
<i>Strongylura marina</i> Atlantic needlefish *	0.0	(0.00)	0.1	(0.05)	0.0	(0.00)	0.0	(0.00)	1		
<i>Syngnathus louisianae</i> Chain pipefish *	0.0	(0.00)	0.1	(0.05)	0.0	(0.00)	0.0	(0.00)	1		

Table 3. (continued)

Taxa	TB		TB Control		LL		LL Control		Total	RA (%)	P
	Impoundment		Mean	S.E.	Impoundment		Mean	S.E.			
	Mean	S.E.			Mean	S.E.					
Total crustaceans	9.0	(3.45)	24.5	(6.20)	9.7	(3.83)	13.9	(3.67)	1414		0.0036
<i>Palaemonetes paludosus</i> Riverine grass shrimp	8.1	(3.05)	6.4	(2.28)	9.6	(3.80)	7.1	(1.87)	791	55.9	NS
<i>Rhithropanopeus harrisi</i> Harris mud crab	0.1	(0.06)	15.2	(4.16)	0.0	(0.00)	5.2	(2.06)	500	35.4	0.0001
<i>Farfantepenaeus aztecus</i> Brown shrimp *	0.1	(0.06)	1.9	(0.64)	0.0	(0.00)	0.6	(0.22)	54	3.8	0.0005
<i>Callinectes sapidus</i> Blue crab *	0.0	(0.00)	0.8	(0.24)	0.0	(0.00)	0.2	(0.15)	25	1.8	
<i>Palaemonetes intermedius</i> Brackish grass shrimp	0.6	(0.37)	0.2	(0.15)	0.0	(0.00)	0.4	(0.12)	25	1.8	
Family Cambridae Unidentified crayfish	0.2	(0.16)	0.0	(0.00)	0.0	(0.04)	0.4	(0.21)	13		
<i>Palaemonetes</i> spp. Unidentified grass shrimp	0.0	(0.00)	0.1	(0.05)	0.0	(0.00)	0.1	(0.07)	3		
<i>Alpheus heterochaelis</i> Bigclaw snapping shrimp *	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.1	(0.05)	1		
<i>Hippolyte zostericola</i> Zostera shrimp *	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
<i>Tozeuma carolinense</i> Arrow shrimp *	0.0	(0.00)	0.1	(0.05)	0.0	(0.00)	0.0	(0.00)	1		

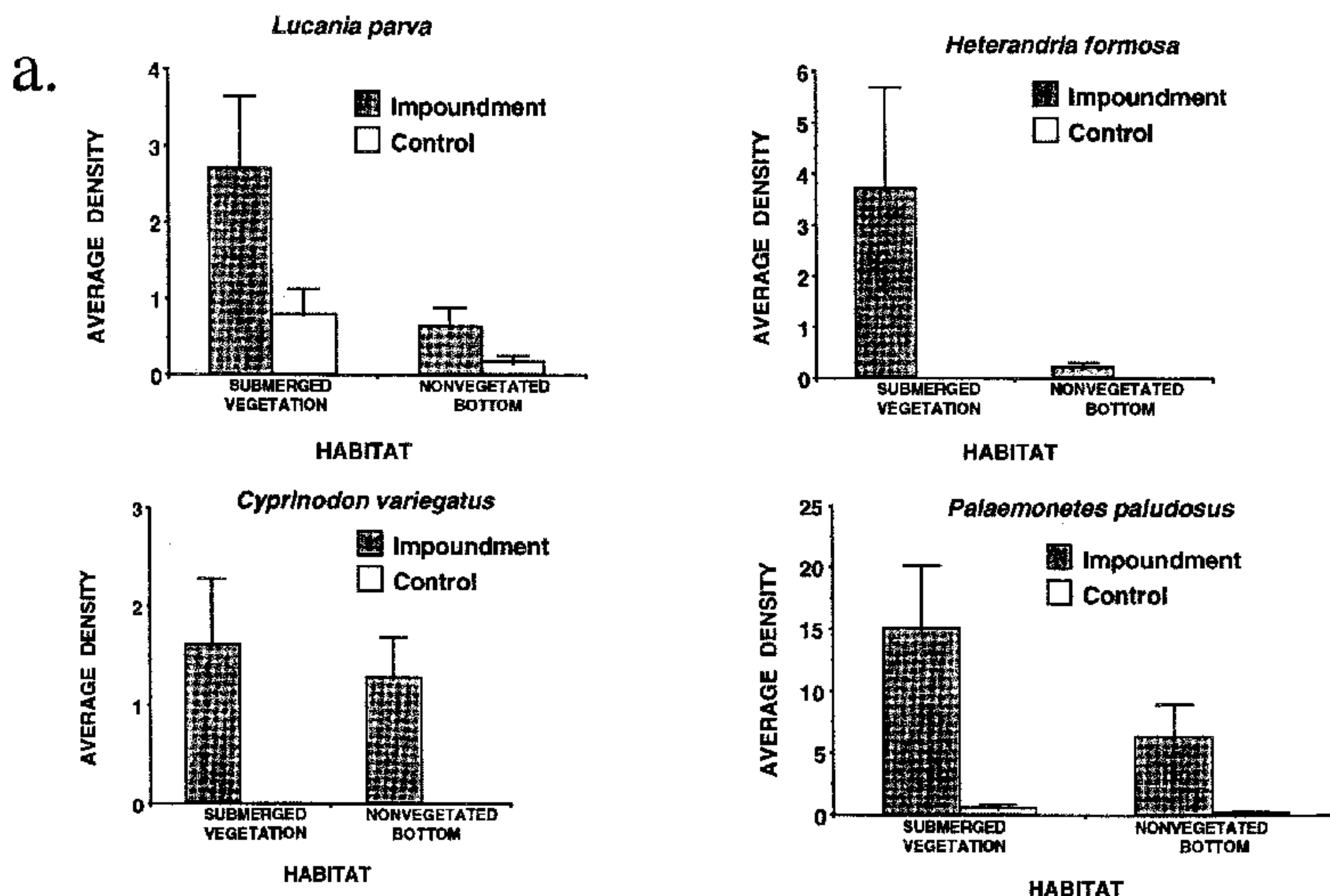
Kensley, 1997) accounted for 98% of the total decapod crustaceans taken in our samples (Table 3). Three species numerically dominated the fish assemblage in ponds, and accounted for 70% of the total. The most abundant species were *Lucania parva*, *Heterandria formosa*, and *Cyprinodon variegatus* (Table 3).

The marsh was inundated in May at TBC, LLI, and LLC. We collected a total of 28 fish and 10 crustacean taxa in May at marsh and pond sample sites (Tables 3 and 4). We found more fishes than crustaceans in ponds (60%, Table 3) and marshes (76%, Table 4). At this time, crustaceans contributed more than fishes to the biomass in ponds (5.5 vs. 4.7 g m⁻² wet weight), whereas fishes yielded more biomass than crustaceans in the marsh (11.5 vs 6.5 g m⁻² wet weight).

The most abundant fishes collected from ponds in May (88% of the total) were *L. parva*, *C. variegatus*, and *Menidia beryllina* (Table 3). *H. formosa*, *L. parva*, and *C. variegatus* were most abundant in marsh samples (Table 4). The dominant crustacean taxa taken from ponds in May, accounting for 95% of the total, were *P. paludosus*, *Rhithropanopeus harrisi*, and *F. aztecus* (Table 3). *P. paludosus* and crayfish (Family Cambridae) were most abundant on the marsh surface (Table 4).

In March, pond densities of total resident taxa and most of the abundant species were significantly greater in managed than unmanaged areas (Tables 2 and 3, Figures 2a and 3a). *L. parva* was significantly more abundant in the managed areas, and *H. formosa* and *C. variegatus* were taken only in managed areas. The densities of *P. paludosus* were significantly greater in the managed areas compared to unmanaged areas. In contrast to this pattern exhibited by estuarine residents, the transient taxa (including all fishery species), which must reproduce outside marsh areas and recruit to this habitat type as young, were more numerous in unmanaged areas (Table 3, Figures 3a and 4a). Total transient taxa and *C. sapidus* densities were significantly greater in unmanaged areas than in the managed areas (Tables 2 and 3). *F. aztecus* was taken exclusively in unmanaged areas, although the number we collected in March was small (Table 3, Figure 4a). The distribution patterns for organism density between areas was mirrored by animal biomass estimates. The mean biomass (g per m²) of the resident taxa was significantly greater in managed than unmanaged areas (ANOVA Contrast, $p < 0.001$; Means-TBI = 1.81 and LLI = 3.76 vs. TBC = 1.06 and LLC = 0.29), whereas the mean biomass of transient taxa was significantly greater in the unmanaged than in the managed areas

MARCH (PRE-DRAWDOWN)



MAY (DURING DRAWDOWN)

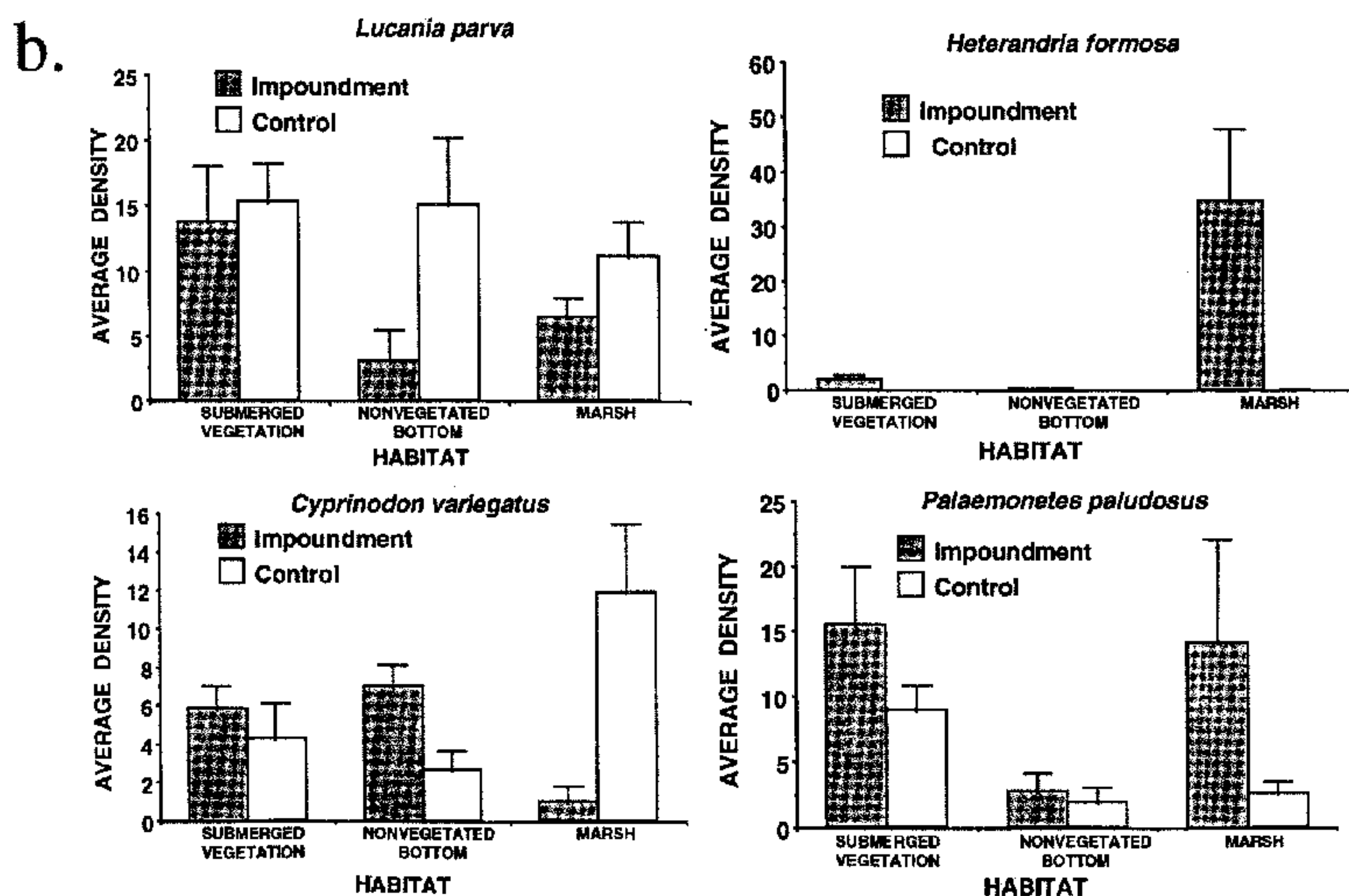


Figure 2. Distribution of abundant resident nekton among habitat types and between impoundments and controls. The average densities (animals m^{-2}) of *Lucania parva* rainwater killifish, *Heterandria formosa* least killifish, *Cyprinodon variegatus* sheepshead minnows, and *Palaemonetes paludosus* riverine grass shrimp are depicted for (a) March and (b) May 1995. The error bars equal ± 1 standard error (S.E.). The mean and S.E. were calculated from the following number of samples: March: Impoundments-SAV = 20, Nonvegetated = 30; Controls-SAV = 32, Nonvegetated = 18; May: Impoundments-SAV = 24, Nonvegetated = 26, Marsh = 7; Controls-SAV = 36, Nonvegetated = 14, Marsh = 14.

Table 4. Mean densities, number m^{-2} , (with standard errors, S.E.) of animals collected on the marsh surface at the Three Bayou (TB) control area and at the Little Lake (LL) impoundment and control areas in May 1995. Each mean and standard error are estimated from 7 samples. The total number of animals collected is given for each taxon and major category (fishes and crustaceans). The relative abundance (RA) of taxa within each major category also is given when it is at least 1%. Transient taxa identified with *

Taxa	TB Control		LL Impoundment		LL Control		Total	RA (%)
	Mean	S.E.	Mean	S.E.	Mean	S.E.		
Total fishes	34.3	(6.61)	45.6	(12.64)	19.4	(6.49)	695	
<i>Heterandria formosa</i> Least killifish	0.0	(0.00)	34.6	(13.32)	0.1	(0.14)	243	35.0%
<i>Lucania parva</i> Rainwater killifish	11.9	(3.61)	6.4	(1.54)	10.3	(4.22)	200	28.8%
<i>Cyprinodon variegatus</i> Sheepshead minnow	19.9	(5.63)	1.0	(0.85)	3.9	(1.91)	173	24.9%
<i>Gambusia affinis</i> Western mosquitofish	0.0	(0.00)	1.0	(0.72)	1.4	(0.87)	17	2.4%
<i>Poecilia latipinna</i> Sailfin molly	0.3	(0.29)	1.7	(0.61)	0.3	(0.29)	16	2.3%
<i>Fundulus pulvereus</i> Bayou killifish	0.4	(0.20)	0.4	(0.30)	1.1	(0.60)	14	2.0%
<i>Menidia beryllina</i> Inland silverside	1.4	(1.27)	0.0	(0.00)	0.0	(0.00)	10	1.4%
<i>Gobiosoma bosc</i> Naked goby	0.0	(0.00)	0.0	(0.00)	0.9	(0.86)	6	
<i>Lepomis cyanellus</i> Green sunfish	0.0	(0.00)	0.0	(0.00)	0.9	(0.86)	6	
Family Cyprinodontidae Unidentified killifish	0.0	(0.00)	0.0	(0.00)	0.6	(0.57)	4	
<i>Lepomis microlophus</i> Redear sunfish	0.0	(0.00)	0.3	(0.29)	0.0	(0.00)	2	
<i>Adinia xenica</i> Diamond killifish	0.1	(0.14)	0.0	(0.00)	0.0	(0.00)	1	
<i>Elops saurus</i> Ladyfish *	0.1	(0.14)	0.0	(0.00)	0.0	(0.00)	1	
<i>Fundulus similis</i> Longnose killifish	0.1	(0.14)	0.0	(0.00)	0.0	(0.00)	1	
<i>Micropterus salmoides</i> Largemouth bass	0.0	(0.00)	0.1	(0.14)	0.0	(0.00)	1	
Total crustaceans	4.6	(1.54)	15.4	(8.52)	11.6	(3.17)	221	
<i>Palaemonetes paludosus</i> Riverine grass shrimp	1.1	(0.55)	14.1	(7.98)	4.1	(1.63)	136	61.5%
Family Cambridae Unidentified crayfish	0.0	(0.00)	1.3	(0.64)	7.1	(2.01)	59	26.7%
<i>Rhithropanopeus harrisii</i> Harris mud crab	2.4	(1.09)	0.0	(0.00)	0.0	(0.00)	17	7.7%
<i>Farfantepenaeus aztecus</i> Brown shrimp *	0.4	(0.30)	0.0	(0.00)	0.0	(0.00)	3	1.4%
<i>Callinectes sapidus</i> Blue crab *	0.1	(0.14)	0.0	(0.00)	0.1	(0.14)	2	
<i>Uca longisignalis</i> Gulf marsh fiddler crab	0.1	(0.14)	0.0	(0.00)	0.1	(0.14)	2	
<i>Palaemonetes pugio</i> Daggerblade grass shrimp	0.1	(0.14)	0.0	(0.00)	0.0	(0.00)	1	
<i>Uca</i> spp. Unidentified fiddler crab	0.1	(0.14)	0.0	(0.00)	0.0	(0.00)	1	

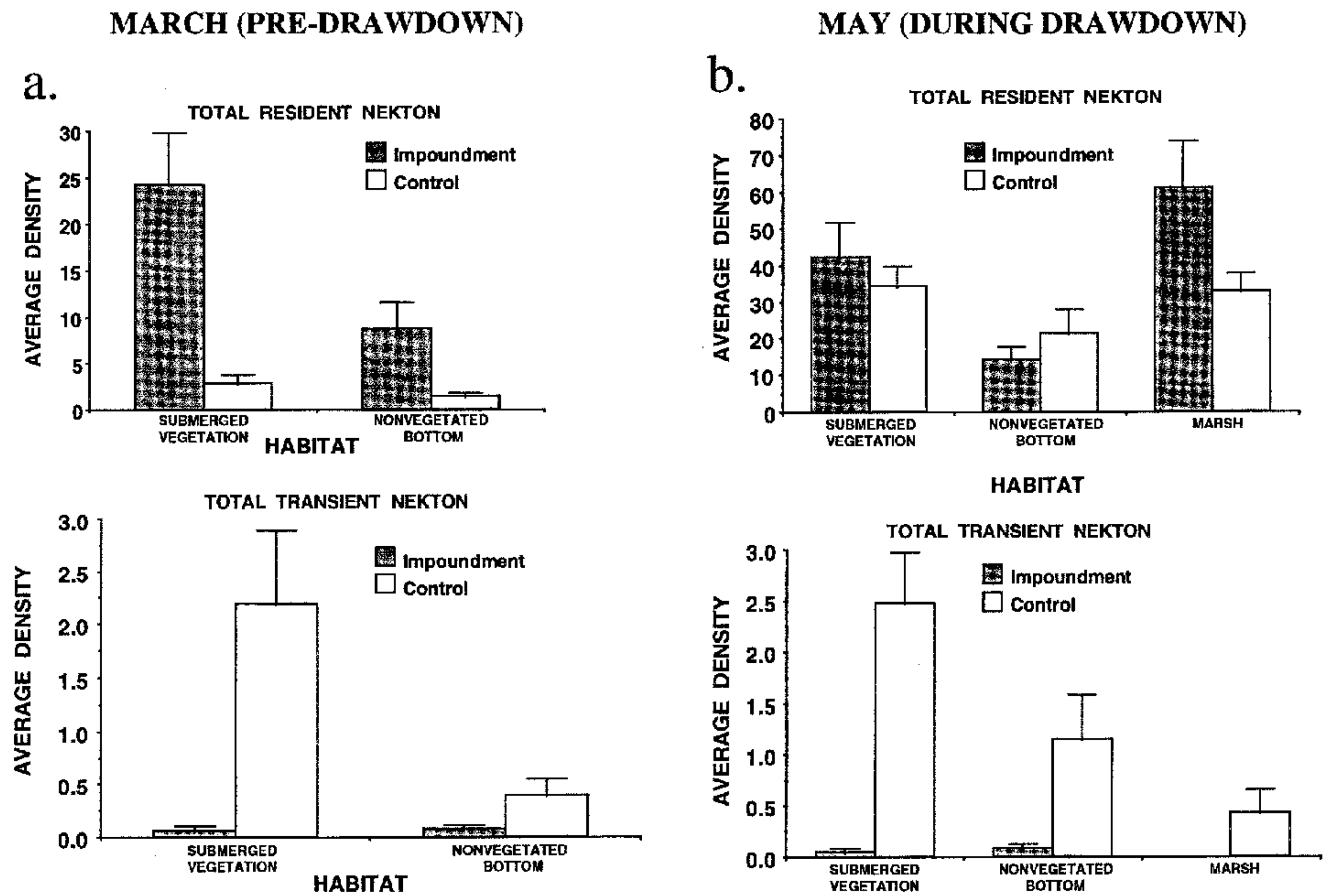


Figure 3. Distribution of resident and transient nekton among habitat types and between impoundments and controls. The average densities (animals m^{-2}) are illustrated for (a) March and (b) May 1995. Error bars equal ± 1 standard error (S.E.). The number of samples used to determine mean and S.E. are given in Figure 2.

(ANOVA Contrast, $p = 0.007$; Means-TBC=0.89 and LLC=0.26 vs. TBI=0.05 and LLI=0.04).

The nekton distributions also were significantly affected by habitat type in March. The total resident and total transient nekton (Table 2), as well as *L. parva* (ANOVA Habitat Effect, $p < 0.001$), were significantly more abundant at sites containing submerged vegetation than at nonvegetated sample sites (Figures 2a and 3a). *C. sapidus* also had higher mean densities in SAV than over bare pond bottom, although the main effect of Habitat was not significant at the 0.05 level in the ANOVA for this species ($p = 0.052$). There was, however, a significant interaction between Location and Habitat in the analysis ($p = 0.031$). *C. sapidus* was more abundant in SAV than on nonvegetated bottom in controls, but few of these organisms were taken in either habitat type inside managed areas (Figure 4a). Similarly, *H. formosa* was more numerous in SAV than at nonvegetated sites, but only in managed areas; this species was not collected in the unmanaged areas (Figure 2a).

In May, pond densities of total resident taxa and total fishes were not significantly different in managed and unmanaged areas (ANOVA Location Effect, $p > 0.53$), whereas total crustacean densities in ponds were greater in unmanaged than managed areas (Table 3). Although *C. variegatus* was more numerous in managed than unmanaged areas, *L. parva* was more abundant in unmanaged than managed areas, and densities of *P. paludosus* in the two treatments were not significantly different (ANOVA Location Effect, $p = 0.64$, Table 3; Figure 2b). Densities of total transient taxa, *F. aztecus*, and *R. harrisii* in May were significantly greater in unmanaged than managed areas (Tables 2 and 3; Figures 3b and 4b). These results for total transient taxa and *R. harrisii* were confirmed using a Games-Howell post-hoc comparison (both control means were significantly greater than the two impoundment means). The Games-Howell analysis for *F. aztecus* showed that densities in the TBC were significantly greater than those in either impoundment, but densities in LLC and LLI were

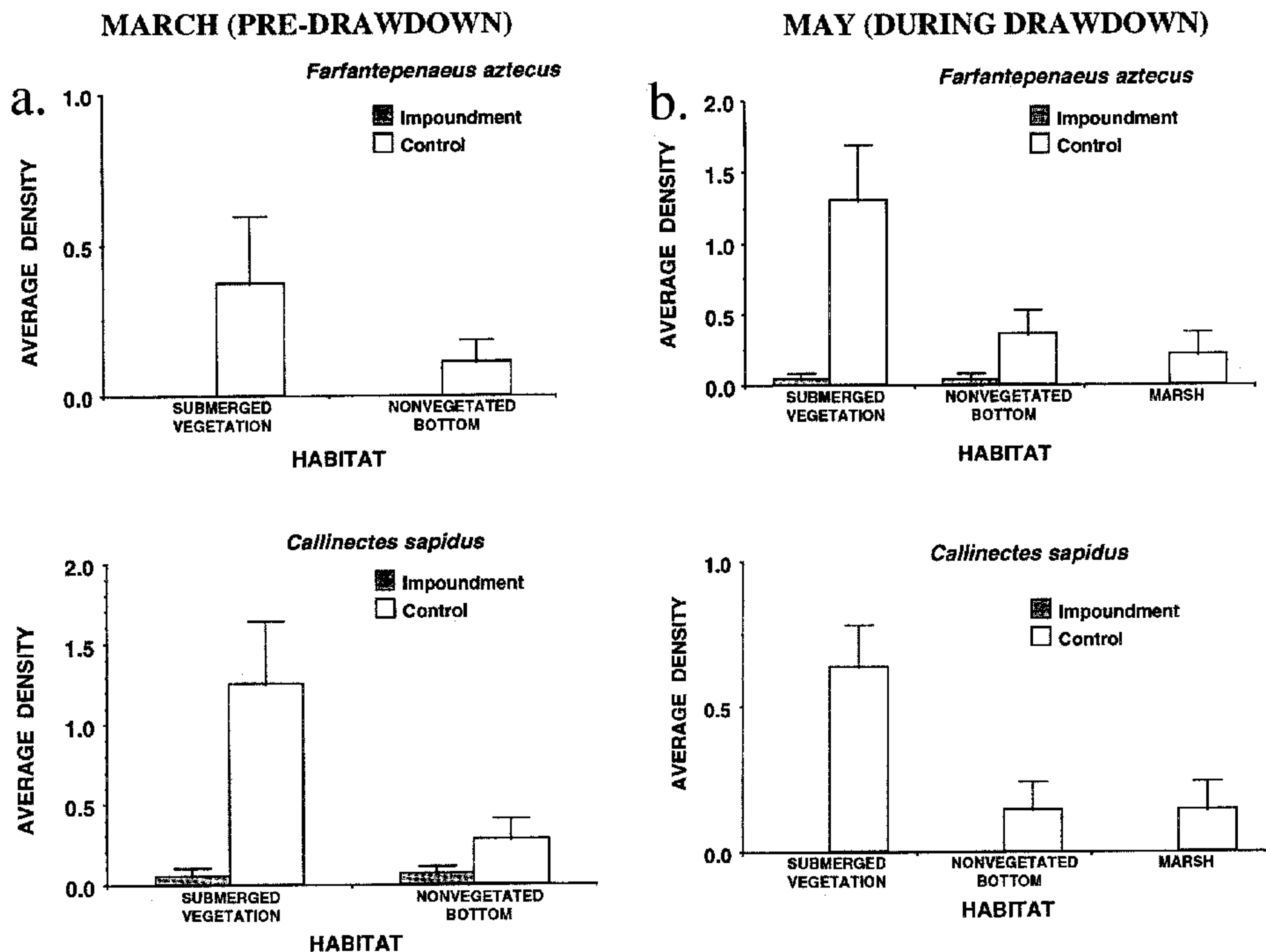


Figure 4. Distribution of abundant transient species among habitat types and between impoundments and controls. Average densities (animals m^{-2}) of *Farfantepenaeus aztecus* brown shrimp and *Callinectes sapidus* blue crabs are shown for (a) March and (b) May 1995. The error bars equal ± 1 standard error (S.E.). The number of samples used to determine the mean and S.E. are given in Figure 2.

not significantly different. The mean biomass estimates of the transient taxa were significantly greater in unmanaged than managed areas (ANOVA Contrast, $p < 0.001$; Means-TBC=7.67 and LLC=3.16 vs. TBI=0.10 and LLI=0.00), whereas the biomass estimates of the resident taxa were not significantly different between treatments (ANOVA Contrast, $p = 0.86$; Means-TBC=8.30 and LLC=8.92 vs. TBI=6.88 and LLI=6.01).

The habitat type influenced animal distributions in May, as well. The densities of *L. parva* (ANOVA Habitat Effect: $p = 0.002$) and *P. paludosus* (ANOVA Habitat Effect: $p < 0.001$) were significantly greater in SAV than at nonvegetated sites (Figure 2b). *C. sapidus* (in controls) and *H. formosa* (at LLI) had higher mean densities in SAV than at sites lacking vegetation (Figures 2b and 4b). Marsh-surface densities of numerically dominant resident species (e.g., *L. parva*, *C.*

variegatus, *H. formosa*, and *P. paludosus*) were similar to, or in some cases greater than, overall densities in pond habitats (Tables 3 and 4; Figure 2b). *F. aztecus* and *C. sapidus*, however, were less abundant on the marsh surface than in SAV contained within ponds (Tables 3 and 4; Figure 4b).

The standing crops (number or biomass of animals per ha) of fishery species were substantially greater in the unmanaged areas than in the managed areas (Table 5). The number and biomass of *C. sapidus* (March) and *F. aztecus* (May) in the unmanaged areas were an order of magnitude greater than in managed areas. The standing stocks of fishery species other than *C. sapidus* and *F. aztecus* were low in the unmanaged areas, but these species were not collected in managed areas.

Comparisons of physical characteristics among marsh locations are in Table 6. In general, the man-

Table 5. Estimated standing crop in numbers and biomass (g wet weight) for selected species in one hectare at each location. Values were calculated separately for March and May. Estimates were derived for each location by multiplying the mean density or biomass in marshes and ponds by the areal coverage of that habitat type and dividing by the total area. Biomass values are in parentheses

Taxa	Normalized standing crop			
	Triple Bayou Impoundment	Triple Bayou Control	Little Lake Impoundment	Little Lake Control
<i>March</i>				
Transient Species				
<i>Callinectes sapidus</i>	450 (270)	5649 (2730)	215 (220)	1775 (895)
<i>Farfantepenaeus aztecus</i>	0 (0)	2040 (71)	0 (0)	197 (4)
<i>Brevoortia patronus</i>	0 (0)	471 (12)	0 (0)	789 (47)
<i>Micropogonias undulatus</i>	0 (0)	0 (0)	0 (0)	394 (95)
<i>Paralichthys lethostigma</i>	0 (0)	157 (24)	0 (0)	0 (0)
Resident Species				
<i>Palaemonetes paludosus</i>	11928 (1829)	1569 (161)	93751 (12719)	2169 (241)
<i>Lucania parva</i>	13053 (3730)	2511 (553)	3225 (994)	1972 (544)
<i>Heterandria formosa</i>	450 (17)	0 (0)	16772 (860)	0 (0)
<i>Cyprinodon variegatus</i>	7202 (2116)	0 (0)	8063 (4510)	0 (0)
<i>May</i>				
Transient Species				
<i>Farfantepenaeus aztecus</i>	450 (540)	9865 (20477)	0 (0)	2169 (4694)
<i>Callinectes sapidus</i>	0 (0)	4007 (19780)	0 (0)	2444 (15027)
Resident Species				
<i>Lucania parva</i>	73369 (11422)	114423 (16521)	48007 (17865)	143739 (27391)
<i>Cyprinodon variegatus</i>	40961 (10724)	136753 (51915)	34728 (14850)	39134 (12362)
<i>Menidia beryllina</i>	15079 (2003)	14176 (4106)	4516 (3559)	5522 (1736)
<i>Heterandria formosa</i>	0 (0)	0 (0)	170620 (11420)	866 (24)
<i>Palaemonetes paludosus</i>	45462 (9329)	32054 (8367)	117224 (22152)	52896 (18370)
<i>Rhithropanopeus harrisii</i>	450 (968)	74196 (8170)	0 (0)	20511 (2311)

Table 6. The environmental characteristics of sample locations. Mean and (± 1 standard error, S.E.) are given for parameters measured in marsh ponds at impoundment and control locations (TB = Three Bayou; LL = Little Lake) sampled in March and May 1995. Each mean and standard error are estimated from 25 samples (except means and standard errors for Vegetation Cover were estimated using data from randomly-selected sample sites only; in March LLC = 20 and in May TBC = 20 and LLC = 20 for this parameter). *P* values also are given for impoundment vs. control contrasts for parameters in which the main effect of LOCATION was significant

Taxa	TB Impoundment		TB Control		LL Impoundment		LL Control		<i>P</i>
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	
<i>March</i>									
Salinity (ppt)	5.0	(0.11)	4.8	(0.09)	3.3	(0.12)	4.4	(0.12)	0.0004
Oxygen (ppm)	6.5	(0.26)	7.1	(0.29)	6.6	(0.31)	7.1	(0.32)	
Water temperature (°C)	26.1	(0.59)	24.1	(0.34)	27.5	(0.31)	25.9	(0.48)	0.0004
Water depth (cm)	17.3	(1.79)	32.4	(2.41)	18.6	(1.32)	32.1	(2.42)	0.0001
Turbidity (FTU)	39.4	(9.31)	38.0	(13.74)	24.7	(6.57)	13.6	(1.91)	0.8089
Distance to edge (m)	3.5	(0.59)	3.0	(0.44)	3.5	(0.59)	2.8	(0.85)	
Vegetation cover (%)	10.9	(5.27)	5.0	(2.16)	21.6	(7.01)	6.8	(4.06)	0.0008
<i>May</i>									
Salinity (ppt)	3.0	(0.04)	2.4	(0.10)	1.0	(0.04)	2.0	(0.00)	0.0044
Oxygen (ppm)	6.5	(0.60)	6.8	(0.59)	6.2	(0.68)	6.3	(0.24)	
Water temperature (°C)	32.6	(0.69)	29.9	(0.46)	31.1	(0.46)	29.0	(0.42)	0.0001
Water depth (cm)	24.7	(2.40)	47.2	(3.06)	32.3	(1.33)	59.1	(2.37)	0.0001
Turbidity (FTU)	6.1	(1.26)	3.0	(0.52)	7.3	(1.51)	2.5	(0.41)	0.0013
Distance to edge (m)	4.6	(1.27)	4.5	(0.66)	2.0	(0.13)	6.7	(0.98)	0.0053
Vegetation cover (%)	15.6	(6.49)	55.5	(10.17)	10.0	(4.23)	44.8	(10.12)	

aged areas were shallower and had higher water temperatures than the unmanaged areas, but the dissolved oxygen levels did not differ significantly between these two areas. The salinities were higher at TB than LL. In March and May, mean salinities were lower in the managed than unmanaged area at LL, but lower in the unmanaged than managed area at TB (Table 6). Turbidity levels were not significantly different between areas in March, but were higher in managed areas than in unmanaged areas in May. The areal coverage of SAV was greater in managed areas compared to the unmanaged areas in March. However, in May, after the drawdowns had been in effect for two months, there was no significant difference in SAV coverage between managed and unmanaged areas (Table 6).

Discussion

Marsh areas under structural marsh management supported much lower densities and standing stocks of fishery species than in the adjacent control areas, both at the beginning of, and two months into, the

drawdown period. Although the water-control structures were open before drawdowns were initiated on March 16, water exchange in the managed areas during this pre-drawdown period was still less than in unmanaged areas. Results from our March samples represent pre-drawdown conditions, and these data indicate that recruitment into the managed areas was reduced even when the structures were fully open. *C. sapidus* densities in March were an order of magnitude higher in unmanaged than managed areas. *F. aztecus*, *Brevoortia patronus*, *Micropogonias undulatus*, and *Paralichthys lethostigma*, although much less abundant than *C. sapidus* in March, were taken exclusively in the unmanaged areas.

The water-control structures used at TBI and LLI, variable-crest flap-gated structures, functioned like fixed-crest weirs when the flap-gates were fully open (i.e., when drawdown was not in effect), and studies of marshes managed with fixed-crest weirs show a similar reduction in access (recruitment) and standing crop of fishery species. Recruitment of postlarval *F. aztecus* at Marsh Island, Louisiana was much lower in a marsh managed with fixed-crest weirs than in an

unmanaged marsh, and weekly estimates of *F. aztecus* standing crop in the weir-managed marsh were 25% of that in the marsh without weirs (Herke et al., 1987). In another study conducted in southwest Louisiana, the use of fixed-crest weirs reduced export from a managed marsh 68–80% for *F. aztecus*, 39–68% for *C. sapidus*, and 80–93% for *B. patronus* (Herke et al., 1992). Knudsen et al. (1989) also documented that a weir-managed marsh produced fewer individuals and less biomass of *F. aztecus* at emigration than a nearby unmanaged marsh.

The method we used to estimate standing crop in this study provided an important measure of habitat value for fishery organisms. This method incorporated measures of animal densities in all available habitat types and compensated for differences in the proportion of marsh and ponds in managed and unmanaged areas. In addition, these measurements compensated for any effect that fluctuations in water levels had on nekton densities in different habitat types. Structural marsh management in our study reduced standing crop of fishery species by an order of magnitude.

Structural marsh management can affect access of nekton to estuarine nursery areas in different ways and on different scales by influencing direct access, water-column access, temporal access, and habitat access. Direct access is related to the amount or volume of water exchanged between a marsh system and the surrounding watershed. Levees and water-control structures restrict direct access of nekton by reducing this water exchange (Montague et al., 1987; Rogers et al., 1994). The young of most fishery species are carried into marsh systems as plankton, thus decreasing water exchange will reduce the number of marine fishery organisms recruited into a marsh area (Rogers et al., 1992a; Hoese and Konikoff, 1995). This relationship was documented in a study by Rogers et al. (1992a) that showed a reduction in fishery production as water exchange was incrementally decreased from using no weir, to a slotted weir, to a low fixed-crest weir, and finally to a fixed-crest weir.

Nekton access to managed areas can also be restricted when structures block part of the water column, allowing only organisms in some portions of the water column to enter or leave a managed area (Rogers et al., 1994). As recruits of marine fishery organisms are transported into nursery habitats by tidal currents, they migrate up and down in the water column (and at times onto the bottom) depending upon the time of day and perhaps direction and speed of the current (Weinstein et al., 1980; Herke et al., 1984;

Rogers and Herke, 1985; Rogers et al., 1994). Thus, restrictions to flow in certain parts of the water column are likely to reduce recruitment. In a practical sense, it may be very difficult to separate effects of reduced exchange from these vertical access effects.

Marine fishery organisms recruit to coastal wetland habitats throughout the year, but different species have distinct seasonal peaks in recruitment (Rogers and Herke, 1985; Hartman et al., 1987). Thus, recruitment of these organisms can be negatively affected if water exchange is restricted during critical periods when recruits are abundantly available (McGovern and Wenner, 1990). Such a reduction in recruitment might occur even if overall water exchange is not severely reduced on an annual basis. Seasonal restrictions in access will also modify species assemblages, and subsequent modifications in ecological interactions may affect fishery production within managed areas. Water exchange is severely restricted during a drawdown period, and new recruits are precluded from entering managed areas at this time, unless the structure somehow malfunctions and is blocked open (Rogers et al., 1992b) or the levees are over-topped. Thus, the nursery function of a managed marsh is severely restricted during a drawdown. Our data show that recruitment of *F. aztecus* and *C. sapidus* was underway in March when a drawdown was initiated, but all recruitment ceased in mid-March after the structures were closed and tidal exchange through the structures was precluded. Not surprisingly, densities of *F. aztecus* and *C. sapidus* in the managed areas were extremely low in May; or in some cases, animals were too rare in the managed areas to be collected.

Another way that fisheries can be affected by hydrological management is through a restriction in habitat access. Marsh management can affect habitat accessibility within impounded areas. By altering water levels, management practices can make habitats such as emergent marsh unavailable to enclosed aquatic animals. Studies in Louisiana and Texas show that many fishery species select for emergent vegetation (when it is available) over subtidal nonvegetated bottom (Zimmerman and Minello, 1984; Zimmerman et al., 1984; Minello and Zimmerman, 1985; Thomas et al., 1990; Zimmerman et al., 1990a,b; Baltz et al., 1993; Rozas and Minello, 1998). Access to emergent marsh vegetation appears important in sustaining productivity of fishery species, and reduced access can reduce growth rates (Zimmerman et al., 1999) and increase mortality (Minello and Zimmerman, 1983; Minello et al., 1989; Thomas, 1989; Minello, 1993).

Animals used the marsh surface in our study area when it was flooded in May, and densities of many species in marsh habitat were at least comparable to those in ponds. However, fishery species in our study were less abundant on the marsh surface than in ponds. Perhaps SAV in ponds provided an alternative, structurally complex habitat, that was preferred by these species, as this habitat type was continually flooded and available for exploitation. The marsh surface in our study area may be used more extensively by fishery organisms when SAV is not present due to winter senescence (i.e., late fall through early spring).

Low water levels within managed areas that commonly occur during drawdowns also increase densities of enclosed aquatic animals; these high densities may further reduce growth and increase mortality rates. In addition, many estuarine species require access to refuges from extremes in temperature and from low dissolved oxygen. By restricting movement into and out of managed areas, escape from these conditions may be prevented and mortality increased (Rogers and Herke, 1985; McGovern and Wenner, 1990; Rogers et al., 1992a). We did not observe adverse environmental conditions in these experimental managed areas, but Yakupzak et al. (1977) reported fish kills in managed areas caused by algal blooms and low dissolved oxygen concentrations during the summer.

In contrast to its negative effect on fishery species, structural marsh management generally has a positive effect on the standing crops of resident species, although emigration from managed areas may be restricted for residents as it is for most species (Rogers et al., 1992b; Rogers et al., 1994). In our study, management appeared to benefit estuarine resident species, at least prior to initiation of the drawdown. Most estuarine residents were significantly more abundant in managed than unmanaged areas in March. After the drawdown was in effect for two months, the abundance of resident species was similar inside and outside the managed areas. This change in the pattern of greater densities of resident species in managed than unmanaged areas that we observed in March may be attributed to an apparent increase in areal coverage of SAV in the unmanaged areas after March and to no increase of SAV coverage in managed areas during the drawdown. The distributions of *L. parva* and *P. paludosus*, the most numerous resident species we collected in May, are closely associated with flooded vegetation (Weaver and Holloway, 1974; Rozas and Reed, 1994; Castellanos, 1997). Densities of these species in managed areas during the drawdown period may have been lim-

ited by available SAV habitat. In our study, densities of both species were an order of magnitude higher in SAV than over nonvegetated bottom in managed areas.

In addition to assessing the impact of structural marsh management on nekton density and biomass, this study also documents the use of oligohaline habitats by transient marine organisms. Others have documented the presence of these organisms in low-salinity waters (e.g., see review by Rozas and Hackney, 1983; Herke et al., 1987; Rogers et al., 1992b), but few studies have quantified animal densities in oligohaline habitats. Despite the fact that our study area is > 30 km from open Gulf waters, the estimated average standing crops (number per hectare) of *C. sapidus* and *F. aztecus* in unmanaged areas were 3,712 and 1,118, respectively in March and 3,225 and 6,017, respectively in May. The estimated biomass of *F. aztecus* at the Triple Bayou control location was 20.5 kg per hectare in May. In the associated managed area, biomass was reduced by 97% (to 0.5 kg ha⁻¹). The mean densities of *C. sapidus* and *F. aztecus* in our study are comparable to the densities of these two species reported for SAV, marsh, and nonvegetated bottom from oligohaline areas in Texas at Trinity Bay (Zimmerman et al., 1990a) and Lavaca Bay (Zimmerman et al., 1990b).

In summary, our study shows that restricting water exchange to marsh areas under structural marsh management diminishes the recruitment and standing stocks of fishery species that must migrate from nearshore or offshore spawning sites to marsh nursery areas. The practice of drawing down a management area essentially eliminates recruitment of fishery species into the area and may result in a complete loss of the area's nursery function during the time that a drawdown is in effect. In addition, even when water-control structures are open, the densities of fishery species are reduced inside the managed areas. These negative effects on fishery production might be partially offset by long-term benefits of structural marsh management if this technique enhances emergent wetlands and reverses marsh loss. However, a recent review of the effectiveness of structural marsh management found no evidence that this technique reduced wetland loss in Louisiana (Boyer, 1997). In contrast to the negative effect of management on fishery species, resident fish and crustacean populations seem to flourish in managed areas when a drawdown is not in effect. Following two months of a drawdown, however, populations of residents appeared similar inside and outside managed areas. Increases in SAV occurred outside the

managed areas during our study period, but not inside the managed areas. Because many resident species were closely associated with SAV, the effect of management on SAV may have been responsible for the distribution patterns of resident species.

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References

- Baltz, D.M., Rakocinski, C. and Fleeger, J.W. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environ. Biol. Fish.* 36: 109–126.
- Boesch, D.F., Josselyn, M.N., Mehta, A.J., Morris, J.T., Nuttle, W.K., Simenstad, C.A. and Swift, D.J.P. 1994. Scientific Assessment of Coastal Wetland Loss, Restoration and Management in Louisiana. *J. Coastal Res. Special Issue, No. 20*. v + 103 pp.
- Boyer, M.E. 1997. The effect of long-term marsh management on land-loss rates in coastal Louisiana. *Environ. Mgmt.* 21: 97–104.
- Britsch, L.D. and Dunbar, J.B. 1993. Land loss rates: Louisiana coastal plain. *J. Coastal Res.* 9: 324–338.
- Castellanos, D.L. 1997. Nekton use of submerged aquatic vegetation, marsh, and shallow unvegetated bottom in a Louisiana tidal freshwater ecosystem. M.S. Thesis, University of Southwestern Louisiana, Lafayette. 79 pp.
- Cowan, J.H., Jr., Turner, R.E. and Cahoon, D.R. 1988. Marsh management plans in practice: Do they work in coastal Louisiana, USA? *Environ. Mgmt.* 12: 37–53.
- Hartman, R.D., Bryan, C.F. and Korth, J.W. 1987. Community structure and dynamics of fishes in a Southeast Texas estuary. U.S. Fish and Wildlife Service, Albuquerque, NM. 116 pp.
- Herke, W., Rogers, B. and Grimes, J. 1984. A study of the seasonal presence, relative abundance, movements, and use of habitat types by estuarine-dependent fishes and economically important decapod crustaceans on the Sabine National Wildlife Refuge. Final report for Cooperative Agreement FWS No. 14-16-0009-79-1003 between the U.S. Dept. of the Interior, Fish and Wildlife Service and Louisiana State University. Louisiana Cooperative Fishery Research Unit, Louisiana State University Agricultural Center. 111 pp.
- Herke, W.H., Wengert, M.W. and LaGory, M.E. 1987. Abundance of young brown shrimp in natural and semi-impounded marsh nursery areas: relation to temperature and salinity. *Northeast Gulf Sci.* 9: 9–28.
- Herke, W.H., Knudsen, E.E., Knudsen, P.A. and Rogers, B.D. 1992. Effects of semi-impoundment of Louisiana marsh on fish and crustacean nursery use and export. *N. Am. J. Fish. Mgmt.* 12: 151–160.
- Hoese, H.D. and Konikoff, M. 1995. Effects of marsh management on fisheries organisms: the compensatory adjustment hypothesis. *Estuaries* 18: 180–197.
- Jordan, F., Coyne, S. and Trexler, J.C. 1997. Sampling fishes in vegetated habitats: effects of habitat structure on sampling characteristics of the 1-m² throw trap. *Trans. Am. Fish. Soc.* 126: 1012–1020.
- Knudsen, E., Paille, R., Rogers, B. and Herke, W. 1989. Effects of a fixed-crest weir on brown shrimp *Penaeus aztecus* growth, mortality, and emigration in a Louisiana coastal marsh. *N. Am. J. Fish. Mgmt.* 9: 411–419.
- Kushlan, J.A. 1981. Sampling characteristics of enclosure fish traps. *Trans. Am. Fish. Soc.* 110: 557–562.
- McGovern, J.C. and Wenner, C.A. 1990. Seasonal recruitment of larval and juvenile fishes into impounded and non-impounded marshes. *Wetlands* 203–221.
- Minello, T.J. 1993. Chronographic tethering: a technique for measuring prey survival time and testing predation pressure in aquatic habitats. *Mar. Ecol. Prog. Ser.* 101: 99–104.
- Minello, T.J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of Essential Fish Habitat. *In*: Benaka, L. (ed.). *Fish Habitat: Essential Fish Habitat and Habitat Rehabilitation*. American Fisheries Society, Symposium 22: 43–75.
- Minello, T.J. and Zimmerman, R.J. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. *J. Exp. Mar. Biol. Ecol.* 72: 211–231.
- Minello, T.J. and Zimmerman, R.J. 1985. Differential selection for vegetative structure between juvenile brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*), and implications in predator-prey relationships. *Est. Coast. Shelf Sci.* 20: 707–716.
- Minello, T.J., Zimmerman, R.J. and Czapla, T.C. 1989. Habitat-related differences in diets of small fishes in Lavaca Bay, Texas, 1985–1986. NOAA Technical Memorandum, NMFS-SEFC-236. 16 pp.
- Montague, C.L., Zale, A.V. and Percival, H.F. 1987. Ecological effects of coastal marsh impoundments: a review. *Environ. Mgmt.* 11: 743–756.
- Penland, S., Mendelssohn, I., Wayne, L. and Britsch, D. 1996. Natural and human causes of coastal land loss in Louisiana. Coastal Studies Institute and Wetland Biogeochemistry Institute, Louisiana State University, Baton Rouge. 25 pp.
- Perez-Farfante, I. and Kensley, B. 1997. Penaeoid and sergestoid shrimps and prawns of the world; keys and diagnoses for the families and genera. *Mémoires du Muséum National d'Histoire Naturelle, Tome 175*, 233 pp.

- Reed, D.J., De Luca, N. and Foote, A.L. 1997. Effect of hydrologic management on marsh surface sediment deposition in coastal Louisiana. *Estuaries* 20: 301–311.
- Rogers, B.D. and Herke, W.H. 1985. Estuarine-dependent fish and crustacean movements and weir management. In: Bryan, C.F., Zwank, P.J. and Chabreck, R.H. (eds.). *Proceedings of the Fourth Coastal Marsh and Estuary Management Symposium*. pp. 201–219. Louisiana State University Agricultural Center, Louisiana Cooperative Fish and Wildlife Research Unit, Baton Rouge, LA.
- Rogers, B.D., Herke, W.H. and Knudsen, E.E. 1992a. Effects of three different water-control structures on the movements and standing stocks of coastal fishes and macrocrustaceans. *Wetlands* 12: 106–120.
- Rogers, D.R., Rogers, B.D. and Herke, W.H. 1992b. Effects of a marsh management plan on fishery communities in coastal Louisiana. *Wetlands* 12: 53–62.
- Rogers, D.R., Rogers, B.D. and Herke, W.H. 1994. Structural marsh management effects on coastal fishes and crustaceans. *Environ. Mgmt.* 18: 351–369.
- Rozas, L.P. and Hackney, C.T. 1983. The importance of oligohaline estuarine wetland habitats to fisheries resources. *Wetlands* 3: 77–89.
- Rozas, L.P. and Reed, D.J. 1994. Comparing nekton assemblages of subtidal habitats in pipeline canals traversing brackish and saline marshes in coastal Louisiana. *Wetlands* 14: 262–275.
- Rozas, L.P. and Minello, T.J. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries* 20: 199–213.
- Rozas, L.P. and Minello, T.J. 1998. Nekton use of salt marsh, seagrass, and nonvegetated habitats in a south Texas (USA) estuary. *Bull. Mar. Sci.* 63: 481–501.
- Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. 2nd Edition, W. H. Freeman and Co., San Francisco, CA. 859 pp.
- Thomas, J.L. 1989. A comparative evaluation of *Halodule wrightii* Aschers, *Spartina alterniflora* Loisel and bare sand as nursery habitat for juvenile *Callinectes sapidus* (Rathbun). M.S. thesis, Texas A&M University, College Station. 119 pp.
- Thomas, J.L., Zimmerman, R.J. and Minello, T.J. 1990. Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texas bays. *Bull. Mar. Sci.* 46: 115–125.
- Turner, R.E. 1997. Wetland loss in the northern Gulf of Mexico: multiple working hypotheses. *Estuaries* 20: 1–13.
- U.S. Department of Commerce. 1997. Fisheries of the United States, 1996. Current Fishery Statistics No. 9600. Fisheries Statistics Division, Silver Spring, MD. 169 pp.
- Weaver, J.E. and Holloway, L.F. 1974. Community structure of fishes and macrocrustaceans in ponds of a Louisiana tidal marsh influenced by weirs. *Contr. Mar. Sci.* 18: 57–69.
- Weinstein, M.P., Weiss, S.L., Hodson, R.G. and Gerry, L.R. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. *Fish. Bull. U.S.* 78: 419–436.
- Yakupzak, P.M., Herke, W.H. and Perry, W.G. 1977. Emigration of juvenile Atlantic croakers, *Micropogon undulatus*, from a semi-impounded marsh in southwestern Louisiana. *Trans. Am. Fish. Soc.* 106: 538–544.
- Zimmerman, R.J. and Minello, T.J. 1984. Densities of *Penaeus aztecus*, *P. setiferus* and other natant macrofauna in a Texas salt marsh. *Estuaries* 7: 421–433.
- Zimmerman, R.J., Minello, T.J., Castiglione, M. and Smith, D. 1990a. Utilization of marsh and associated habitats along a salinity gradient in Galveston Bay. NOAA Technical Memorandum, NMFS-SEFC-250. 68 pp.
- Zimmerman, R.J., Minello, T.J. and Rozas, L.P. 1999. Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the Northern Gulf of Mexico. In: Weinstein, M.P. (ed.), *Concepts and Controversies in Tidal Marsh Ecology*. New Jersey Sea Grant, Fort Hancock (in press).
- Zimmerman, R.J., Minello, T.J., Smith, D. and Castiglione, M. 1990b. The use of *Juncus* and *Spartina* marshes by fisheries species in Lavaca Bay, Texas, with reference to effects of floods. NOAA Technical Memorandum, NMFS-SEFC-251. 40 pp.
- Zimmerman, R.J., Minello, T.J. and Zamora, G. 1984. Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston Bay salt marsh. *Fish. Bull. U.S.* 82: 325–336.